AN INVESTIGATION OF POPULATION DYNAMICS, INDIVIDUAL BEHAVIOR AND LEARNING CAPACITY OF PAGURUS SAMUELIS OF CARMEL BAY, CALIFORNIA

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THESIS

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by

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Lieutenant, United States Navy
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ABSTRACT

The population of the hermit crab Pagurus samuelis at Carmel River Beach, Carmel, California, was surveyed and the results were statistically treated to determine the distribution of the species. Groups within the population were observed to evaluate the stability of the groups. The population was found to be contagiously distributed with varying degrees of stability exhibited by the groups. The factors governing stability were the restriction imposed by the microenvironment and the amount of time during which the area containing the crabs was flooded.

Laboratory and field observations of individual behavior showed the species to be of an aggressive nature. The learning capacity of P. samuelis was the subject of an experiment in which the performance of individual crabs in a simple T-maze was evaluated; the experiment showed that the crabs were capable of improving their performance with time.

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I. INTRODUCTION

A. GENERAL

Hermit crabs are among the most numerous and easily observable inhabitants of the tide pools along the rocky coast line in the vicinity of Monterey, Pacific Grove and Carmel, California. A general description of hermit crabs can be found in any good text concerning the fauna of the intertidal zone, e.g. MacGinitie and MacGinitie (1968) or Ricketts and Calvin (1939). Such texts offer keys to the most common species, discussions of the general distribution of the crabs and obvious behavioral patterns such as shell fighting and methods of feeding, but the material is presented more from the view of the naturalist than the research scientist. Relatively little has been written concerning population dynamics, individual behavior or the learning ability of hermit crabs of the central California coast.

B. LOCAL SPECIES OF HERMIT CRABS

Belknap and Markham (1965) found four species of Pagurus inhabiting the intertidal zone of the Monterey Bay region. These are P. hirsutiusculus, P. samuelis, P. granosimanus and P. hemphilli. Pagurus samuelis (42.7%) and P. hirsutiusculus (47.0%) comprise approximately 90% of the total pagurid population, with P. samuelis occupying the uppermost reaches of the intertidal zone, ranging from 0.0 to +3.9 feet. This species was selected for the present study due to the relative ease of observation and collection of the individuals.

Keys used for the identification of species were those of Schmitt (1921) and Putnam and Markham (1965). The generic name Eupagurus may be encountered in some publications, leading to confusion in classification. Hazlett (1966) and others have pointed out that the International Commission on Zoological Nomenclature considers the use of the name unauthorized as a synonym for Pagurus.

C. PREVIOUS STUDIES

The most complete study of hermit crab population and individual behavior to date is that of Hazlett (1966), who observed the crabs of the island of Curacao in the Caribbean Sea. Hazlett's statistical treatment of the populations of several species of hermit crabs provided guidelines for the present study and his observations of individual behavior are compared with the behavior of P. samuelis. Crane (1957) made many studies of the individual behavior of the fiddler crab Uca with particular emphasis on the aggressive behavior of the genus.

Students at the Hopkins Marine Station of Stanford University devoted the summer session of 1965 to a study of the pagurids of the rocky beaches of Pacific Grove, California. The students investigated the distribution of species within the intertidal zone and some aspects of the behavior of hermit crabs. Four papers resulting from the study were used as background for the present investigation.

Belknap and Markham (1965) investigated the vertical and horizontal distribution of the intertidal pagurids. Experiments concerning the

reactions of hermit crabs to various degrees of light and observations of daily cycles were conducted by Ball (1965). The importance of antennae as organs of chemical and tactile reception was investigated by Rollefson (1965). Antennae are important tactile receptors but were found essentially unresponsive to chemical stimuli. Rollefson also reported that blind crabs were unresponsive to food particles placed directly in front of them, indicating the importance of the sense of sight to the animals.

MacGinitie and MacGinitie (1968) reported that a crab inhabiting a gastropod shell in which a hole had been drilled could be caused to vacate the shell by prodding the abdomen of the individual. One such individual became so conditioned to the prodding that the crab vacated the shell each time it was picked up. This instance of conditioning and the experiment of Fink (1941) on the learning capacity of P. longicarpus were the only examples of learning in pagurids found in the literature reviewed.

D. AREAS OF STUDY

A preliminary survey of Monterey Bay, the beaches of Pacific Grove and Carmel Bay led to the choice of the northwestern end of Carmel River Beach as the site of the field observations in the present investigation. The presence of large off-shore rocks which afford protection from large waves and the abundance of P. samuelis in the area made it ideal for the study.

Population distribution, stability of groups within the population and individual behavior were the subjects of field observations. Collections of crabs from the area were made for the observation of individual behavior and experiments of the learning capacity of the species in the laboratory.

II. POPULATION DISTRIBUTION

A. NATURAL POPULATIONS

Natural populations may be uniformly, randomly, or contagiously distributed. Social species, such as ants, termites and bees are contagiously distributed. In this sense, the word contagious implies that the population consists of discrete groups or clumps of individuals with the space between groups containing relatively few individuals. Hazlett (1966) found that the pagurids of the island of Curacao were contagiously distributed, and the initial study of P. samuelis at Carmel River Beach was a determination of the population distribution there.

B. STATISTICAL METHOD

The aim of any method for determination of the distribution of a natural population is to statistically calculate the probability that any two individuals chosen at random from the entire population inhabited the same quadrat. The statistical method employed for P. samuelis was one introduced by Morisita (1959). This method is an extension of work done by Simpson (1949); the basic difference is that with Morisita's method the conclusions drawn about population distribution are not dependent on the size of the quadrats into which the population is divided.

Consider a population divided into m quadrats. The fraction of the population found in the i-th quadrat, m_i, is π_i such that $\sum_{i=1}^{m} \pi_i = 1$. A measure of the diversity of the population, λ, can be found from

$$\lambda = \sum_{i=1}^{m} \pi_i^2 \qquad (1)$$

which takes on values $\frac{1}{m} \leq \lambda \leq 1$. The lower value represents the greatest diversity possible, equal numbers of individuals in each quadrat and a uniform distribution ($\pi_i = \frac{1}{m}$ for all i). The larger value represents complete concentration, all individuals in one quadrat and a contagious distribution. Values between these extremes serve to numerically indicate degrees between uniform and contagious distributions.

Let the number of individuals in quadrat i be n_i (i=1, 2, . . . , m) and $N = \sum_{i=1}^{m} n_i$ be the total number of individuals in the population. Simpson (1949) has shown that λ must be modified to account for dealing with a finite sample. This unbiased estimate of λ is given by Morisita (1959):

$$\delta = \frac{\sum_{i=1}^{m} n_i (n_i - 1)}{N (N-1)} \qquad (2)$$

As N and the number of individuals in a quadrat become large, δ reduces to the expression for λ ($\delta \rightarrow \lambda$ as $N \rightarrow \infty$). In order to allow interaction between individuals to be taken into account, it is necessary to consider pairs of individuals. Now, since $\frac{1}{2}[n_i(n_i-1)]$ is the number of pairs of individuals in quadrat m_i and $\frac{1}{2}[N(N-1)]$ is the number of pairs of individuals in the population, δ is the probability that two randomly chosen individuals occupied the same quadrat.

C. INDEX OF DISPERSION

Morisita (1959) introduced an index of dispersion, I_δ, which is the product of δ and m, the number of quadrats. This index is useful because it has the following properties:

1) If $I < 1$, the population is uniformly distributed.

2) If $I \simeq 1$, the population is normally distributed.

3) If $I > 1$, the population is contagiously distributed.

The index of dispersion can be tested for statistical significance by utilizing the variance ratio, or F, test. Provided suitable but realistic restrictions may be placed on δ, then the F ratio for the population, F_o, is given by

$$F_o = \frac{I_\delta (N-1) + m-N}{m-1} \qquad (3)$$

The F_o calculated from Equation (3) is compared with F_{∞}^{m-1}, obtained from standard statistical tables. If $F_o > F_{\infty}^{m-1}(\alpha)$, the conclusions drawn about the population distribution are statistically significant at the level of confidence (α).

D. SAMPLING METHOD

Since it had been observed that the P. samuelis population tended to form concentrated groups of individuals in shady, moist areas above the water line as the tide receded, two areas were chosen for sampling. One area, 15.25 $m.^2$, was in the portion of the tide pool flooded at low tide; the other, 7.0 $m.^2$, was a strip two meters wide around the border of the pool.

The quadrat size chosen was 0.5 by 0.5 meter. A wooden frame of this size was constructed and all individuals within each 0.25 $m.^2$ were counted. Since hermit crabs in the tide pool moved considerably when disturbed, care had to be taken to ensure that an individual was not included in two adjacent quadrats. Table I contains the assembled data from the tide pool and Table II the data for the border area.

E. RESULTS

Utilizing Equations (1), (2) and $I_\delta = q\delta$, the Index of Dispersion and F_o were computed for each area. Within the tide pool $I_\delta = 2.2$, $F_o = 6.8$ and $F_\infty^{62}(99) = 1.5$. The results for the border area were $I_\delta = 3.4$, $F_o = 6.7$ and $F_\infty^{27}(99) = 1.8$. From these results it can be seen that the P. samuelis population of Carmel River Beach is contagiously distributed and that individuals form more concentrated groups in the area bordering the tide pool. This result had been predicted since crabs on the relatively dry border of the pool must congregate in those areas which are protected from the sun and so retain sufficient moisture to sustain life until the tide rises. The F distribution test on the data shows that the results are statistically significant with a 99% level of confidence.

TABLE I

n	f	nf	n(n-1)	f n(n-1)
0	12	0	0	0
1	13	13	0	0
2	8	16	2	16
3	4	12	6	24
4	3	12	12	36
5	2	10	20	40
6	2	12	30	60
7	3	21	42	126
8	3	24	56	168
9	1	9	72	72
10	3	30	90	270
11	2	22	110	220
12	3	36	132	396
17	1	17	272	272
21	1	21	420	420
23	1	23	506	506
24	1	24	552	552

n is the number of individuals in a quadrat

f is the number of quadrats containing n individuals

TABLE II

n	f	nf	(n(n-1)	f n(n-1)
0	17	0	0	0
1	1	1	0	0
2	2	4	2	4
3	3	9	6	18
4	1	4	12	12
7	1	7	42	42
8	1	8	56	56
14	1	14	182	182
18	1	18	306	306

n is the number of individuals in a quadrat

f is the number of quadrats containing n individuals

III. POPULATION STABILITY

A. BACKGROUND

Having determined that the population of P. samuelis was contagiously distributed, a determination of stability within the population was undertaken. The specific purpose of this investigation was to determine whether groups of crabs remained in or returned to a given area at a particular time in the tidal cycle. The necessity to make observations at the same time each day was dictated by the tendency of groups of crabs to disperse as the incoming tide flooded the area in which they were located.

B. REQUIREMENTS

The basic requirements for the investigation were the identification of groups of crabs and daily observation of the individuals for a period of time sufficient to draw conclusions concerning the stability of the group.

1. Identification of groups of crabs

A method of identification which would be useful for a period of longer than several days was not found in the literature reviewed. Hazlett (1966) used different colors of india ink but found that such marks made individual identification possible for only a few days.

Observations of rocks painted with enamel, latex-based paint, and fingernail polish proved that the latter was relatively permanent in

the intertidal zone, and it was decided that marking of shells with polish would be an effective means of identification. The method is recommended for future studies; shells so marked were easily identified for periods of three weeks, and some marked shells were observed for as long as three months.

Three colors of polish were used and groups of crabs were selected from areas sufficiently separated so that inclusion of an individual with another group was not considered likely. It should be noted that any identification of individual hermit crabs based on marking of gastropod shells introduces the assumption that the crab will not change shells during the period of observation. Such exchanges do occur both in nature and in the laboratory but the frequency is such that they can be ignored.

2. Period of observation

The length of time for which groups were observed depended upon the relative stability of the group. Crabs which exhibited a high degree of stability were observed for longer periods of time than groups which were relatively unstable.

C. SELECTION OF GROUPS

The selection of groups of crabs for the stability study was based on the location of the groups. Six areas, designated A-F, were selected (Figures 1-7). The areas were classified by two parameters, the vertical position in the intertidal zone and the degree of restriction of

Figure 1. Sketch of the rocky area at the western end of Carmel River Beach illustrating the positions of Areas A-E.

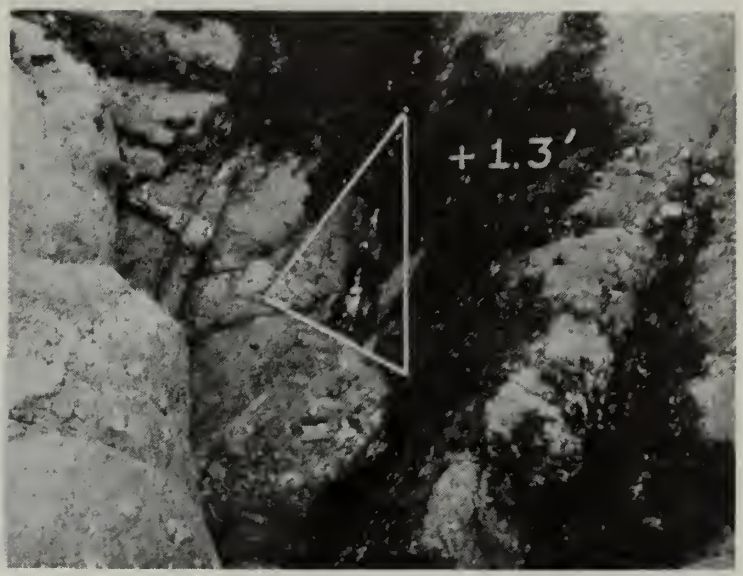


Figure 2. Area A

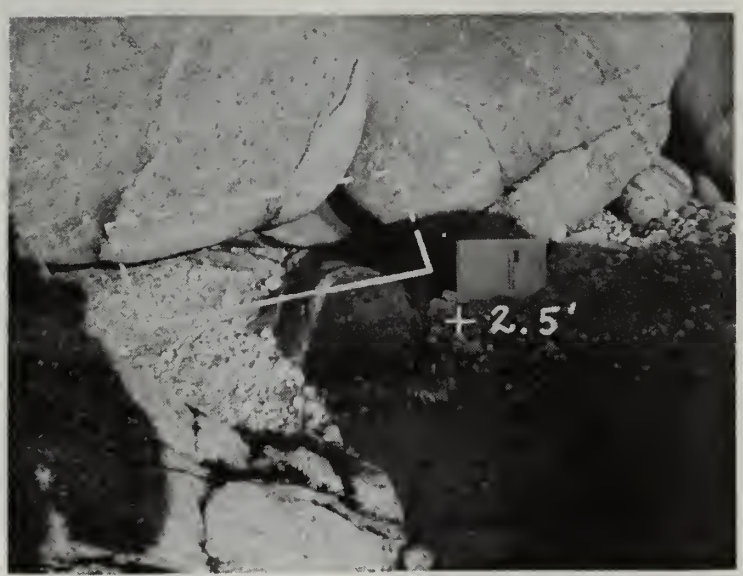
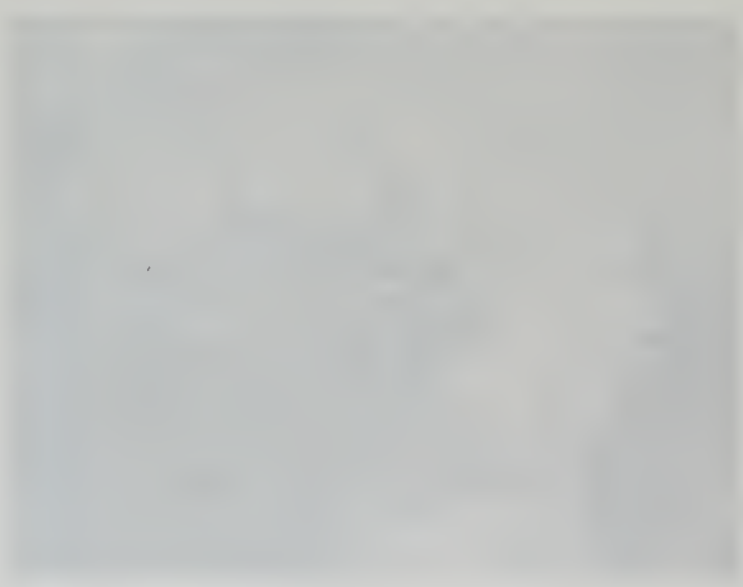


Figure 3. Area B



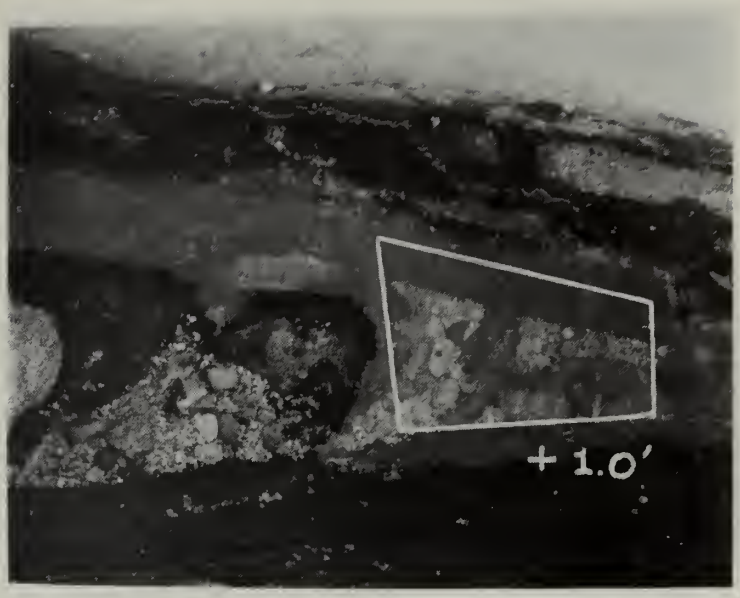


Figure 4. Area C

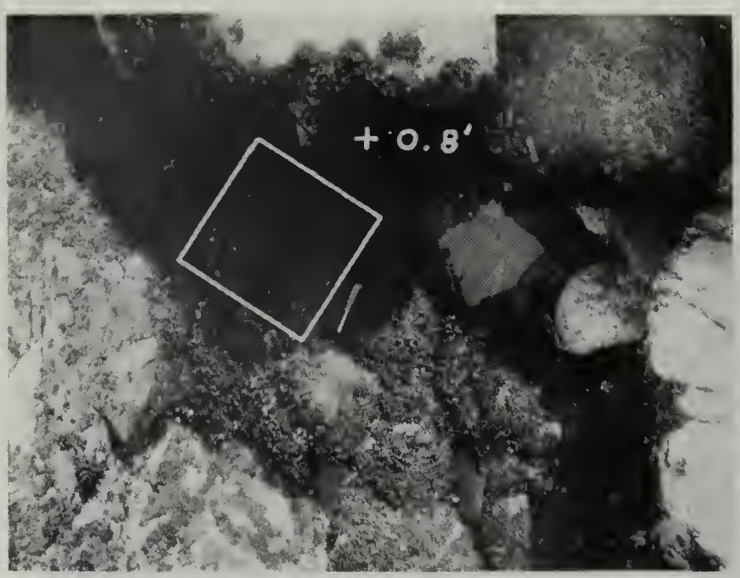


Figure 5. Area D

Figure 6. Area E

Figure 7. Area F

movement imposed by the surroundings. An open area was defined as one in which no restrictions existed, a closed area as one surrounded by rocks or vertical walls which made horizontal movement from the area difficult.

1. Description of areas

Area A, an open area, was located at +1.3 feet and measured 625 cm.^{2}. Flooded at the time of observation, the substrate within the area was smooth rock. The group in Area A consisted of 20 individuals and was observed for eight days.

Area B, measuring 2000 cm.^{2}, located at +2.5 feet, was dry at the time of the observations. The area was rectangular, open on one side, with a pebble substrate. Two groups, designated B-1 and B-2, were observed for 17 and eight days respectively.

Area C, in a crevice at +1.0 feet, was closed. The substrate was smooth rock covered with algae. The area measured 600 cm.^{2} and was flooded during observations. The group in Area C was observed for 17 days.

Area D, an open area of 2500 cm.^{2} on an algae-covered flat rock, was awash at the time of the observations. The area was located at +0.8 feet and the group within the area was observed for 13 days.

Area E, at +0.5 feet, was a flooded, open area measuring 3250 cm.^{2}. The substrate, as that of Area B, consisted of pebbles. The group within the area was observed for 13 days.

Area F was much like Area B. Located at +2.0 feet, the area was open on one side with a pebble substrate. The area was dry during the observations, which continued for eight days.

D. DATA AND RESULTS

Three categories of data were tabulated: number of individuals in the area, number out of the area and the distance moved from the border, and number lost.

In order to obtain the most meaningful comparison of the stability of the groups, all data were treated at the end of the eighth day. The mean number of individuals remaining in each area during the eight days was calculated and the result expressed as a percentage of the original group. Figure 8 is a graphic representation of the results.

Groups A, B-1, C, D and E were taken from their respective areas, marked for identification and immediately replaced in the area. The order of relative stability of these groups was C, B-1, D, E and A (Figure 8). Groups C and B-1 were markedly more stable than the other groups. The higher degree of stability is believed to be governed by two factors, the degree of physical restraint imposed by the surroundings and the amount of time the area was flooded.

Area C, surrounded by vertical walls, was the most restricted area considered in the study. The walls of the crevice entrapped water so that the area was always flooded. Individuals of Group C were active at all times but the walls of the crevice prevented movement beyond the limits of the area.

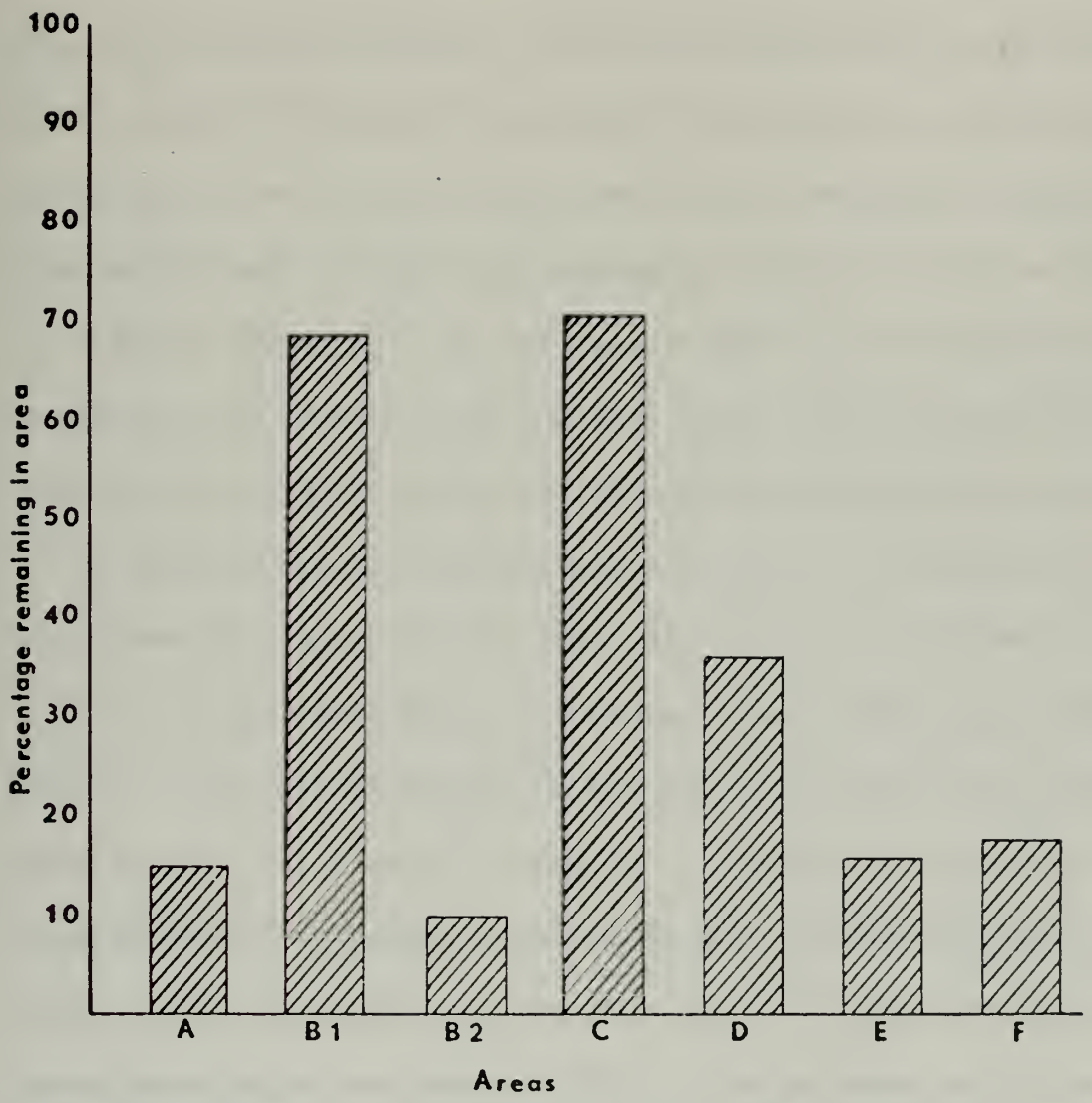


Figure 8. Percentage of individuals in original area after eight days

Area B was the highest area considered and was always dry at the time of the daily observations. The most important factor in the stability of group B-1 was the lack of water for long periods of time. The group was observed on four occasions as the incoming tide flooded the area to determine whether the individuals remained in the area throughout the day. These observations showed that the crabs were dormant during the time when the area was dry, became active as the first waves inundated the area and evacuated the area shortly thereafter.

A typical sequence of events was recorded on 12 August 1970, with 42 individuals in Area B at low tide. The first waves reached the area at 1330, at which time the crabs became active, moving about within the area. By 1400 ten individuals had moved out of the area a mean distance of 17 cm. from the boundaries. The final observation, at 1445, revealed that 37 crabs had evacuated the area. A mean distance from the area was not calculated at this time due to the presence of breaking waves which made observation difficult. The following day 36 crabs were recorded within the area at low tide, proving that the individuals of Group B-1 did evacuate the area during high tide and return prior to low tide.

Group D exhibited intermediate stability. The daily observations of this group were made when the rock upon which they were located was partially submerged. The individuals were always active, apparently feeding upon material within the algae covering the rock. As the water receded the crabs were observed to take positions within the algae and

become dormant. Since Area D was flooded for longer periods of time than Area B, the conclusion is that the longer period of activity accounted for the lower stability of Group D.

Areas A and E were open and flooded at the time of the observations. The groups occupying these areas were the least stable observed during the initial phase of the study. Most individuals moved out of the area immediately upon being replaced following marking. An interesting observation made with both groups was that virtually all of the individuals which could be located each day were found in nearby clusters of algae. This, coupled with observations of the P. samuelis population in general, led to the conclusion that algae plays an important part in the food chain of the species, either directly or as the habitat of other organisms upon which the crabs feed.

The relatively high degree of stability observed in Group B-1 was believed to be the result of one of two factors; either the individuals of the group were attracted to one another or to some physical aspect of the area. Hazlett (1966) found that groups of P. miamensis migrated short distances when rocks upon which they aggregated were relocated, indicating that individuals were more attracted by physical factors than other members of their group.

In order to determine which of these factors is more important in P. samuelis, another group, designated Group B-2, was collected from an area near Area E and relocated in Area B. It was expected that the group would remain in the new location if conspecific attraction was

more important or that the group would migrate back to the original location if stability was governed by the attraction of a specific physical area.

Figure 8 shows that Group B-2 was very unstable in the new location. The group evacuated the new area but did not return to the original location. The only conclusion which can be drawn from this observation is that conspecific attraction appears to be of little consequence in P. samuelis. No valid conclusion concerning the importance of attraction to a particular area or object can be inferred. It is believed that the relocation of the group was to an area too far removed from the original location. The distance involved was approximately four meters; Hazlett's conclusions on the subject were drawn from an experiment in which the group had to migrate only 0.1 meter. Further observations and experimentation are required before the importance of the physical attraction of an area can be adequately evaluated.

The final phase of the investigation of group stability was directed toward a determination of the importance of the time factor on stability. Specifically, it was designed to determine whether a group of crabs, known to have been relatively stable, would retain the stability if they were removed from the area for an extended period of time.

Group F, located in an area similar to Area B, was observed for ten days and found to be quite stable. Twenty-seven individuals of the original 35 (79%) remained in Area F at the end of the ten days. The group was collected on 17 November 1970 and taken to the laboratory

where the crabs were used for learning experiments and observations of individual behavior.

Sixteen of the crabs were returned to Area F on 26 January 1971 and the group was observed through 3 February 1971. The stability of the group was adversely effected (Figure 8), but it cannot be stated with certainty that the time factor was dominant. It was observed that crabs in the laboratory began molting and fighting for shells after approximately five weeks of confinement. The reason for this behavior will be explained in the discussion of individual behavior. It is possible that the crabs of Group F evacuated the area in search of more suitable shells.

IV. INDIVIDUAL BEHAVIOR

A. GENERAL

Because of the nature of the distribution of P. samuelis, individuals repeatedly come into contact with other members of their group. When such contact is made, three types of behavior can occur. The individuals may take no notice of one another, they may react aggressively or, if of opposite sex and appropriate physiological condition, sexual activity may result. If aggressive behavior takes place it may be divided into two phases; the initial or posturing phase, followed by actual physical contact.

Physical damage of a serious nature is rare since the body of hermit crabs is protected by the gastropod shell. If intensive fighting occurs, one or more legs may be lost, but this does not result in permanent disability due to the regenerative process characteristic of the crustacea.

B. PROCEDURE

Observations of individual behavioral patterns were made in the field and in laboratory aquaria. Field observations were made as the opportunity arose, with no schedule as to time of day or tidal cycle.

Crabs observed in the laboratory were those used for learning experiments. Two aquaria were utilized, one for housing the crabs and the other for feeding and conducting the learning experiments. All observations of behavior were made in the housing aquarium as it was assumed that the presence of food would alter the behavioral patterns

of the crabs. Observations of feeding crabs proved this assumption valid; individuals frequently fought over bits of food.

1. Reactions observed

Initial observations revealed seven reactions which were repeated frequently and were chosen as the basis for the investigation. These reactions were:

a. Negative reaction. Crabs appeared to take no notice of one another.

b. Antennal agitation. The antennae of the crabs were moved rapidly in circular fashion.

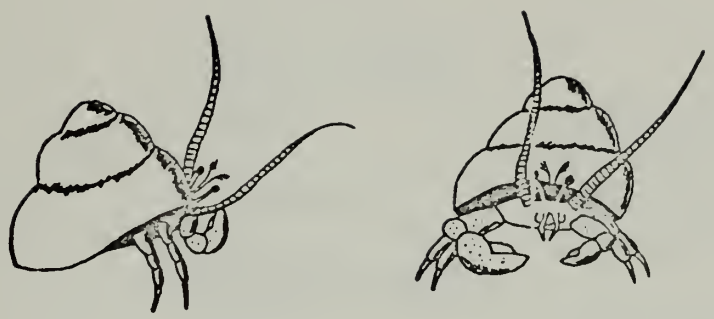
c. Cheliped presentation. One or both of the chelipeds were moved into a position roughly parallel with the surface. Figure 9 illustrates the normal and extended position of the chelipeds.

d. Ambulatory raise. One of the ambulatory legs is raised through an arc of 60° to 90°, as illustrated in Figure 9.

e. Withdrawal. One of the crabs retreated from the other following posturing.

f. Shell seizure. One crab, designated the attacker, seized the shell of the other, designated the defender. This is one aspect of shell fighting.

e. Cheliped rapping. A defensive reaction which occurred when shell fighting took place. The major cheliped of the defender was rapidly and repeatedly brought down on the interior of the shell, just inside the aperature.



Normal Posture

Cheliped Presentation

Ambulatory Raise

Figure 9. Pagurus samuelis, normal posture and two agressive signals.

2. Summary of data

The following observations were recorded:

Total reactions	
Field	205
Laboratory	442
Negative reaction	
Field	64 (31.2%)
Laboratory	136 (30.8%)
Antennal agitation	
Field	118 (57.5%)
Laboratory	284 (64.4%)
Cheliped presentation	
Field	102 (49.7%)
Laboratory	228 (51.5%)
Ambulatory raise	
Field	33 (16.1%)
Laboratory	68 (15.4%)
Withdrawal	
Field	66 (32.2%)
Laboratory	134 (30.4%)
Shell seizure	
Field	14 (6.8%)
Laboratory	80 (18.2%)

Cheliped rapping	
Field	6 (2.9%)
Laboratory	48 (10.9%)

C. RESULTS

There was no significant difference between field and laboratory behavioral patterns with the exception of the reactions associated with shell fighting. The reason for this difference is believed to be the result of the presence of ample food in the laboratory. Crabs were normally fed every second or third day, and after approximately five weeks some individuals began to molt.

1. Shell fighting

Hermit crabs must exchange shells throughout their adult life as they molt and become too large for the shell occupied. The presence of sufficient food enabled all crabs to grow rapidly; the result was molting and the subsequent desire to exchange shells. It is interesting to note that the aggressive crab in a shell fight was apparently unable to distinguish between a shell larger than his own and one of smaller size. Of the 94 shell fights recorded, 57 involved the larger crab as the attacker. Had these encounters resulted in the expulsion of the defender, the attacker could not have used the new shell.

Shell fighting commenced with the approach of the attacker toward the defender. This was the manner in which other encounters occurred. Approach was most often from the front of the defender but

approaches from other directions was not uncommon. The two crabs entered the posturing phase of the encounter, most often commencing with antennal agitation, believed to be important in the recognition process of the species. Typical posturing included cheliped presentation and/or the ambulatory raise. The encounter to this point was typical of all one-on-one interactions, and it was at this time that it became apparent that a shell fight was to take place.

Following posturing the attacker seized the shell of the defender and turned the crab over, manipulating the defender into the opposed position in which the aperatures of the two shells lie face to face (Figure 10). The defender had always withdrawn into his shell by this time and cheliped rapping followed in 57.5% of the fights observed. This defensive measure did not deter the attacker; it is believed that cheliped rapping serves only to make known the fact that the shell is occupied.

In the opposed position the attacker grasped the shell of the defender as illustrated in Figure 10. The chelipeds of the attacker were inserted into the opposed aperature but seizure of the defender was not observed as reported in P. longicarpus by Allee and Douglis (1945).

Successful completion of a shell fight resulted when the attacker raised his shell and brought it down rapidly on the shell of the defender, producing an audible clicking sound. This procedure was repeated in a series of ten to twelve raps after which the defender vacated his shell climbed on top of it.

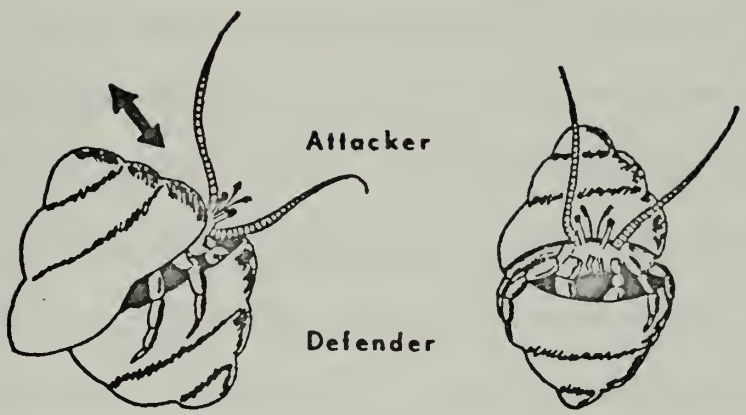


Figure 10. Pagurus samuelis, opposed position in shell fighting.

The attacker, having evicted the defender, left his own shell and entered the shell of the defeated crab, always maintaining a grasp on his own shell. If the new shell proved satisfactory the attacker released his old shell and retired. The defeated crab then entered the discarded shell of the attacker. This exchange of shells was undoubtedly facilitated by the fact that the combatants observed were of approximately the same size.

2. Comparison with Hazlett's observations

The method of shell fighting described here is similar to that of the pagurids observed by Hazlett (1966), who also made a quantitative determination of the number of successful shell fights in one species of the family Diogenidae, Clibanarius tricolor. He reported that 45.5% of the fights observed in this species were successful. The percentage of successful fights observed in P. samuelis was much lower (3.2%) but it is not believed that any valid conclusions can be formulated on the basis of observation of the two species. It is obvious that based on the available data, successful shell fights involving P. samuelis are rare.

Two of the posturing patterns of P. samuelis, the cheliped presentation and ambulatory raise, were also noted and quantitatively described by Hazlett. In his investigation the cheliped presentation was described as either a major or a minor presentation, a distinction not made in the present study. Hazlett also noted two types of ambulatory raises, single or double raises. The number of ambulatory legs involved in the raise was the basis for the distinction between the single and double raise.

Hazlett reported that the cheliped presentation occurred in 67.6% of the ambulatory raise in 48.4% of the confrontations of three species of Paguridae, P. miamensis, P. bonairensis and P. marshi. The corresponding figures for P. samuelis are 51.1% and 15.6% respectively. The difference in the number of cheliped presentations is not believed to be significant and could be the result of visual interpretation or observation technique. The large difference between Hazlett's ambulatory raises and those of P. samuelis is considered of consequence; P. samuelis differs from the other pagurids studied with respect to this particular reaction.

D. SUMMARY

A general conclusion concerning the individual behavior of P. samuelis is that it is an aggressive species, particularly when food or the exchange of shells is the stimulus triggering aggressive action. The importance of these stimuli was noted when the crabs were feeding and after individuals began to molt. The crabs are notably aggressive even when food is not present, as evidenced by the fact that only 31% of the one-on-one interactions observed resulted in a negative reaction.

V. LEARNING CAPACITY

A. BACKGROUND

Experiments conducted for the purpose of evaluating the learning capacity of hermit crabs have been few. Wells (1965) gives an excellent review on the subject of learning in marine invertebrates, citing one such experiment. The experiment, conducted by Fink (1941), involved the tendency of P. longicarpus to withdraw into the shell in response to taps of the side of the aquarium in which the individuals were kept. Fink discovered that the crabs became conditioned to the tapping and that the mean number of withdrawals decreased with time. Thirty individuals were used for the experiment, the mean number of withdrawals decreased from approximately 11 to one over an 18 day period, and considerable individual variability was noted. The most responsive crab withdrew 173 times during the 18 days, the least responsive only six times.

B. EXPERIMENTAL METHOD

The method of experimentation utilized in the present investigation was a simple T-maze (Figure 11). Two similar aquaria were used (Figure 12); the crabs were housed in one aquarium while the second was reserved for feeding the crabs and for conducting trials in the maze.

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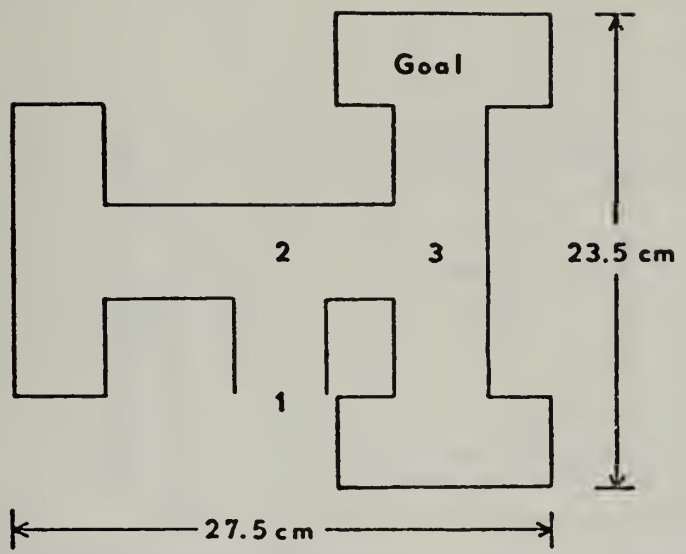

Figure 11. Maze used for learning experiment. Points 1, 2 and 3 are the positions at which a decision had to be made.

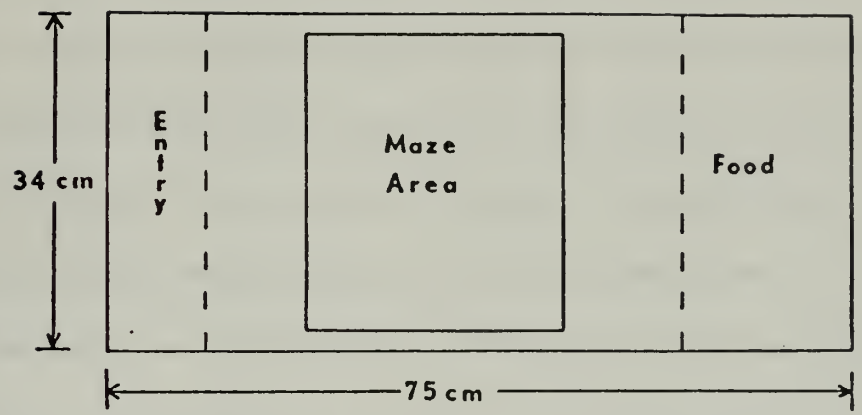

Figure 12. Feeding/Maze aquarium. A second aquarium of similar dimension was used for housing the crabs.

There were two reasons for utilizing the second aquarium:

1) Food was used as the reward for successful completion of the maze. It was believed that the crabs would have more desire for the reward if they were not allowed to feed in the housing aquarium.

2) One phase of the experiment was to determine whether hermit crabs could transfer previous experience gained in one situation to the solving of another problem. In order to evaluate the effect of previous experience on negotiating the maze, three groups of crabs were allowed to feed in the second aquarium before the maze was placed in the aquarium. The crabs were released in that portion of the aquarium designated as the entry area (Figure 12) and had to move to the opposite end of the aquarium to obtain food. When the maze was placed in the aquarium it was positioned so that the general direction of movement through the maze was the same as that taken by the crabs in attaining food previously.

1. Maze trials

The maze was constructed of light-weight modeling plastic and designed so that three correct decisions were required for successful passage through the maze. At the beginning of each trial, the crab was placed in position 1 (Figure 11). The initial decision was either entry into the maze or a move to the left, right or rear, away from the entrance. An error at this point was designated an initial error to distinguish it from errors committed within the maze, either reversals of direction or a wrong turn at positions 2 or 3, which were designated

subsequent errors. A crab committing an initial error was immediately replaced in position 1. Once the individual entered the maze no further physical stimulus was employed unless the crab returned to the entrance and exited from the maze. A crab exiting the maze was again replaced at the entry point. An arbitrary time limit of 20 minutes was imposed on each trial; if the crab had not reached the goal by this time he was returned to the housing aquarium.

Food used as the reward was boiled beef, pork, chicken or shrimp. Crabs showed no preference for a particular type of food, evidence of their role as scavengers in nature. When a crab completed the maze the individual was allowed to remain with the reward for three minutes and was then transferred to the feeding area of the aquarium to make the maze ready for the next individual; two crabs were never allowed in the maze at the same time. Following 30 minutes of feeding, the crab was returned to the housing aquarium. Care had to be taken to ensure that crabs returning to the housing aquarium had no food in their chelipeds or mouth parts, for an individual with food was immediately attacked by the other crabs.

2. Data recorded

Three categories of data were recorded for each trial conducted during the experiment. These were the mean errors per successful trial, the mean time required per successful trial and the percentage of the group completing the maze. If a crab failed to complete the maze on a given trial his performance was not included in the compiling of the first two categories of data.

Fifty-two individuals, divided into five groups, were used in the experiment. The original intent was to have each crab complete nine trials, but Group II completed only seven before the crabs began to molt and fight over their shells, as reported in the discussion of individual behavior.

Three hundred ninety-six trials were conducted with 20 (0.5%) of the trials resulting in failure of the crab to complete the maze. Thirteen of the failures occurred in the first five trials, indicating that virtually all of the crabs tested had learned the way through the maze by the sixth trial. The number of failures was so small that it was considered insignificant, but the fact that 65% of the failures occurred in the first five trials and that no crab failed to complete the maze on the final two trials is considered proof that learning did take place.

3. Variability in performance

As was observed by Fink (1941), there was great variability in the performance of the 52 individuals; the greatest number of errors committed by an individual completing nine trials was 51, the least seven. One crab failed to complete the maze on three of the nine trials while 35 individuals always reached the goal within the 20 minute period allowed.

C. RESULTS

The crabs were collected in two large groups of 25 and 27 individuals and subdivided into five groups used in the experiment. Group I consisted

of 12 individuals, Group II of 13, and Groups III, IV and V contained nine crabs each. Prior to the collection of Groups I and II the bottoms of the aquaria were covered with 3-5 cm of clean beach sand in the manner prescribed by Hazlett (1966).

Group I was introduced to the maze three days after collection. Group II was fed in the feeding/maze aquarium three times prior to their first trial in the maze. The performance of these groups is graphically summarized in Figure 13. It can be seen that Group II committed fewer errors and completed the maze more quickly than Group I for the first four trials. The performance of the two groups on trials five, six and seven is not considered significantly different, indicating that the familiarization of Group II with the feeding/maze aquarium might have enabled the individuals to perform better in the initial trials but made little difference once the crabs of Group I became accustomed to the maze.

An interesting behavioral pattern observed in Groups I and II in both the housing and the feeding/maze aquaria resulted in the removal of the sand prior to the collection of Groups III, IV and V. The individuals of Groups I and II frequently picked up grains of sand and other material from the bottom of the aquaria. Since the sand had not been sterilized it was believed that the crabs were obtaining food from the substratum. Individuals within the maze would sit for extended periods of time exploring the sand with their chelipeds and putting small particles in their mouths. This behavior was considered detrimental to the performance of the groups in the learning experiment.

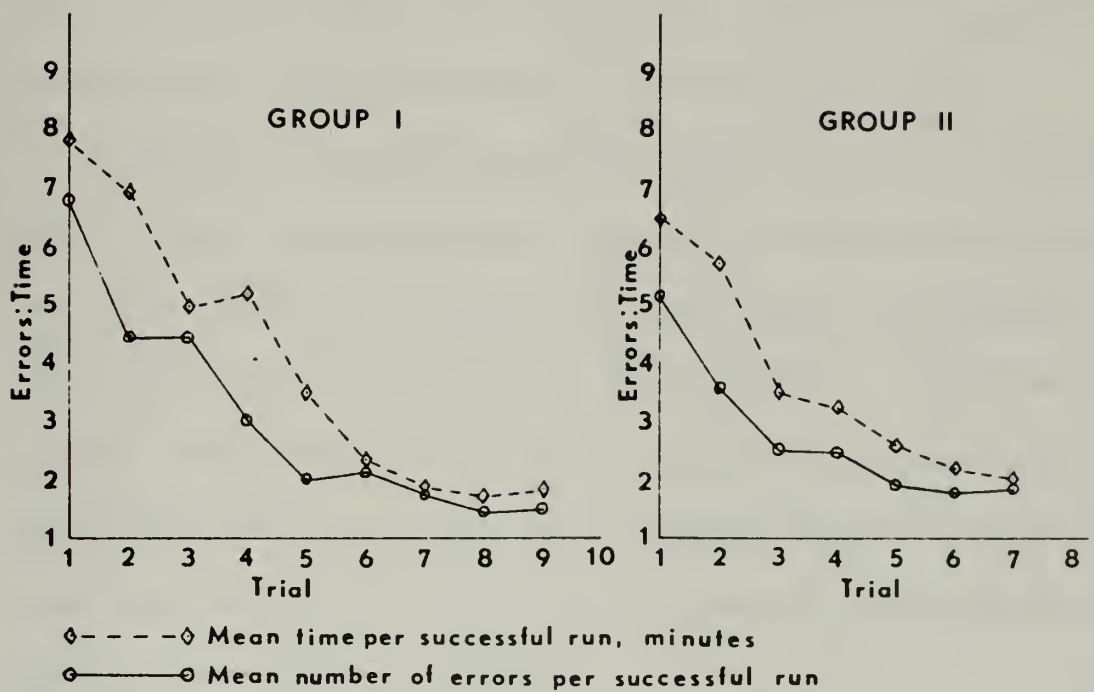

Figure 13. Performance of Groups I and II in the maze. Bottom of aquaria covered with 3-5 cm. of sand.

In order to be able to make a meaningful comparison between the performance of crabs with and without the sand covering in the aquaria, Group III was introduced to the maze with no orientation period in the feeding/maze aquarium and Group IV was fed three times prior to introduction to the maze, a procedure similar to that used with Groups I and II. Group V was fed nine times in the feeding/maze aquarium prior to the group's first trial in the maze. Figure 14 is a graphic representation of the performance of the final three groups.

Comparison of the performance of Groups III, IV and V indicates that the crabs which were familiar with the feeding/maze aquarium made fewer errors and completed the maze in less time than those which were introduced to the maze with no feeding in the second aquarium. Further, comparison of the performance of Groups IV and V shows that the group which had been fed a greater number of times in the feeding/maze aquarium was better qualified to negotiate the maze than the group which received only three feedings.

An attempt to evaluate the effect of the sand on the bottom of the aquaria is less conclusive. Comparison of Groups I and III reveals that while Group III did commit fewer errors (5.6 vs. 6.8) on the initial trial, Group I completed the maze in less time (7.8 vs. 8.1 minutes). Furthermore, Group I committed only 4.40 errors per successful trial on the second trial while Group III committed 5.33. The performance of the two groups on subsequent trials was not significantly different. Similarly, Group IV's performance was only slightly better than that of

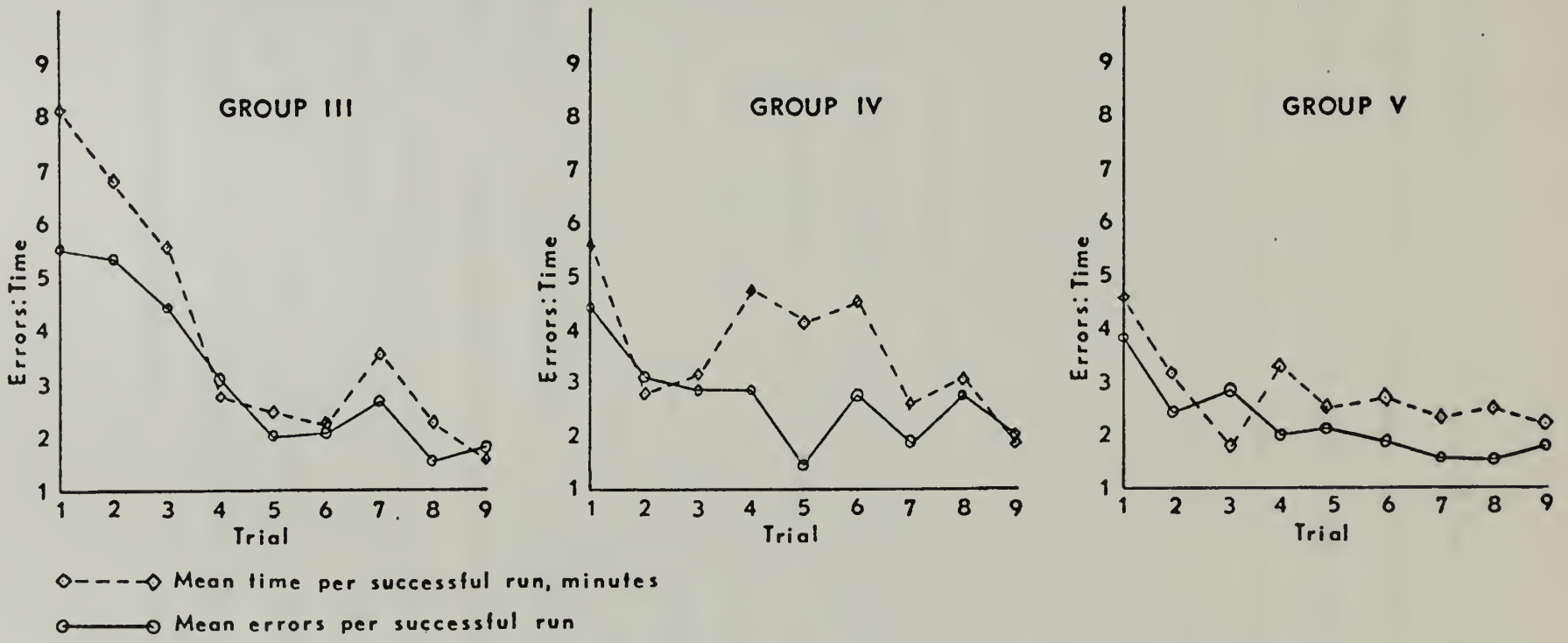

Figure 14. Performance of Groups III, IV, and V in the maze. No sand on the bottom of the aquaria.

Group II for the first two trials, after which the performance of the two groups was almost identical. Individuals of Groups III, IV and V were also observed sitting within the maze while they explored the bottom of the aquarium with their chelipeds. These observations and comparisons of performance lead to the conclusion that the sand on the bottoms of the aquaria did not significantly alter the performance of the crabs.

An examination of Figures 13 and 14 leaves little doubt that learning did take place if one accepts the general definition that learning is the modification of behavior by previous experience. The performance of all five groups improved as the number of trials increased. It can also be said with some confidence that the individuals of Groups II, IV and V were able to transfer the experience of moving from one end of the aquarium to the other in search of food from the feeding situation to the problem with which they were confronted in the maze.

Observations of the crabs within the maze support the contention of Rollefson (1965) that the antennae are important as organs of tactile reception. The antennae were very actively moved along the walls of the maze. When the individual reached a corner the antennae were extended around the corner before the crab progressed onward. In the immediate vicinity of the reward, within four or five centimeters, the sense of sight seemed more important.

VI. FUTURE INVESTIGATIONS

A. COMPARATIVE STUDIES

The investigation of population and individual behavior of P. samuelis raised questions about this and other species which could form the basis for future investigations into the ecology and individual behavior of the pagurids of Carmel Bay.

An investigation which would prove interesting and useful would be a comparative study of one or more of the other Pagurus of the area. Pagurus hirsutiusculus which ranges from - 1.9 to + 2.5 feet in the intertidal zone, is widely distributed at Carmel River Beach, and specimens of P. granosimanus and P. hemphilli were observed in the area. Field observations of the latter two species would prove difficult as their vertical range is well below the normal low tide level. A similar study of any of the species in another area might show that the crabs vary with location as well.

B. POPULATION STABILITY

More observations are required in the area of group stability within the P. samuelis population. It is believed that areas chosen for the present investigation were too small and that the population would prove more stable within areas as large as a tide pool. This assumption is based on the fact that crabs observed typically moved only two to three meters from the borders of the small areas considered.

C. INDIVIDUAL BEHAVIOR

Ricketts and Calvin (1939) reported that egg-bearing female P. samuelis are seen in the Monterey area from April through August. An investigation into individual behavior of the species during the period when sexual activity could result would shed light on several unanswered questions, principally whether copulation can occur only immediately following molting of the female as reported by some investigators; other sources indicate that sexual activity can take place at any time during the mating season.

An unusual occurrence involving reproduction took place during the learning experiment. On 10 January 1971 the crabs which had completed a trial in the maze were being transferred to the housing aquarium via a water-filled dissecting tray to ensure that none were in possession of food particles. One of the crabs was observed repeatedly raising her shell so that about two thirds of her abdomen was exposed. A gelatinous mass was seen on the abdomen, and periodically groups of organisms were released from the mass into the water.

Microscopic observation of these organisms revealed that the crab had given birth to 200 to 300 young. An attempt to keep the larvae alive in a fingerbowl failed; all died within four days.

Further investigation into this subject is believed necessary. Either the sexual cycle was accelerated in the laboratory (higher water temperature is a possible solution) or Ricketts and Calvin were wrong in their assertion that egg-bearing females are seen no earlier than April.

D. LEARNING

In addition to investigating the learning capacity of other species of Pagurus there are numerous experiments which could be conducted using P. samuelis.

These include the effects of various environmental factors, i. e. the effect of light, variations in temperature, variability of performance throughout the day and tidal cycle, etc. The performance of blind individuals or individuals without antennae could be evaluated. Another area of possible investigation is the ability of P. samuelis to distinguish shapes, light or dark articles, and various colors.

The present investigation has proven that learning can take place in hermit crabs; the variations of experimental procedure in this area are restricted only by the ingenuity of the investigator.

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13 ABSTRACT

The population of the hermit crab Pagurus samuelis at Carmel River Beach, Carmel, California, was surveyed and the results were statistically treated to determint ehd distribution of the species. Groups within the population were observed to evaluate the stability of the groups. The population was found to be contagiously distributed with varying degrees of stability exhibited by the groups. The factors governing stability were the restriction imposed by the microenvironment and the amount of time during which the area containing the crabs was flooded.

Laboratory and field observations of individual behavior showed the species to be of an aggressive nature. The learning capacity of P. samuelis was the subject of an experiment in which the performance of individual crabs in a simple T-maze was evaluated; the experiment showed that the crabs were capable of improving their performance with time.

14. KEY WORDS	LINK A		LINK B		LINK C	
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